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Fatty-acid profile of *Lesquerella* germplasm in the National Plant Germplasm System collection

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ABSTRACT

Seeds of *Lesquerella* (Brassicaceae) contain oil rich in hydroxy fatty acids (HFA) that may be used in several industrial products such as motor oils, greases, plastics, cosmetics and pharmaceuticals. One of the most abundant HFA in the seed oil is lesquerolic acid, which is chemically similar to ricinoleic acid from castor (*Ricinus communis* L.). Hence, lesquerolic oil derived from a domestically grown crop could reduce the import of castor oil. In nature, *Lesquerella* grows in open and arid habitats, and therefore it may be an alternative arid-land crop. Domestication and breeding efforts warranted establishing a *Lesquerella* germplasm collection by the USDA-ARS, National Plant Germplasm System (NPGS). Seeds of 195 accessions (32 species) from the collection were evaluated for content of four different HFA (lesquerolic, densipolic, auricolic and ricinoleic) and seven other fatty acids (palmitic, palmitoleic, stearic, oleic, linolenic, linoleic and arachidic) by gas chromatography. The highest content of lesquerolic acid (C20:1 OH) was found in seeds of *L. pallida* and *L. lindheimeri* (average of >80%); the highest content of densipolic acid (C18:2 OH) was in seeds of *L. perforata*, *L. stonensis*, *L. densipila*, *L. lyrata* and *L. lescurii* (average>40%); the highest content of auricolic acid (C20:2 OH) was in *L. auriculata* and *L. densiflora* (average>30%), and the highest ricinoleic acid (C18:1 OH) content was in seeds of *L. densipila*, *L. lescurii*, *L. lyrata* and *L. perforata* (>10%). The highest percentages of the seven other fatty acids evaluated were oleic 23.8 (*L. lasiocarpa*), linoleic 18.7 (*L. ludoviciana*), linolenic 11.4 (*L. cinerea*), stearic 4.9 (*L. densiflora*), palmitic 4.7 (*L. stoniensis*), palmitoleic 2.8 (*L. angustifolia*), and arachidic 1.7% (*L. gordonii* and *L. gracilis*). Fatty-acid composition varied across species and accessions, and was likely influenced by the location and year the seeds were harvested, and by seed color. The NPGS *Lesquerella* collection could potentially serve as a valuable source of germplasm for the crop improvement.

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1. Introduction

Lesquerella (Brassicaceae) seeds contain hydroxylated vegetable oil (25–30%), protein (30%) and gums (Hayes et al., 1995; Dierig et al., 1996; Salywon et al., 2005; Dierig et al., 2006a,b). Vegetable oil from *Lesquerella* has applications in several industrial products, such as: greases, hydraulic fluids, motor oils, drying agents, protective coatings, plastics, cosmetics, polishes, inks and pharmaceuticals (Barclay et al., 1962; Roetheli et al., 1991). The oil is biodegradable and may be used as a lubricity enhancer in diesel fuels (Goodrum and Geller, 2005). Seed meal of *Lesquerella* has nutritional value

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suitable for livestock and poultry feed due to high lysine content (Miller et al., 1962; Carlson et al., 1990; Roetheli et al., 1991). Gums obtained from seed coats may be utilized as gelling and thickening agents in many edible and pharmaceutical products (Holser et al., 2000).

Vegetable oil from *Lesquerella* is rich in hydroxy fatty acids, and the major components of the oil are lesquerolic, densipolic and auricolic acids (Barclay et al., 1962; Hayes et al., 1995; Dierig et al., 1996; Salywon et al., 2005; Finkenstadt et al., 2007; Vaughan and Holser, 2007). Lesquerolic acid (14-hydroxy-*cis*-11-octadecenoic acid: C20:1 OH) is similar to ricinoleic acid (12-hydroxy-octadec-cis-9-enoic acid: 18:1-OH) from castor (*Ricinus communis* L.) which in the last several years has been imported from Brazil, China and India. Deriving lesquerolic acid from a domestically grown *Lesquerella* crop could reduce the import of castor oil to the U.S., decreasing domestic vulnerability to foreign markets (Janick et al., 1996). The other fatty acids play a role in seed oil stability and some are precursors to other fatty acids occurring in *Lesquerella* seeds (Reed et al., 1997; Broun et al., 1998).

Plants in the *Lesquerella* genus are predominantly herbaceous annuals, with some biennial and perennial species, that grow in dry and open habitats (Rollins and Shaw, 1973). In nature, *L. fendleri*, the species with the most agronomically important characteristics, occur in areas with 250–400 mm of rainfall (Thompson et al., 1989; Thompson and Dierig, 1993) which makes it a potential crop suitable for cultivation in southwestern regions of the U.S. (Van Dyne, 1997). Breeding, selection efforts, and agronomic trials have been undertaken to develop *Lesquerella* into an economic crop (Coates, 1994; Nelson et al., 1996; Roseberg, 1996; Dierig et al., 2003; Adam et al., 2007). Seed mass, oil content and hydroxy fatty-acid composition was described for several wild collected accessions which are a part of *Lesquerella* breeding efforts by the USDA-Agricultural Research Service (ARS) in Arizona (Salywon et al., 2005). A publicly available *Lesquerella* germplasm collection is maintained at the, USDA-ARS National Plant Germplasm System (NPGS) at Parlier, CA. The objective of this study was to evaluate the content of selected fatty acids in the seeds of the NPGS *Lesquerella* germplasm collection.

2. Material and methods

The fatty-acid profile (%) was analyzed in seeds of 195 *Lesquerella* accessions (representing 32 species) which are part of a germplasm collection maintained by the NPGS. Seeds used for the analysis were harvested in various years of germplasm regeneration in Pullman, WA, on a sandy loam soil with sprinkler head irrigation (harvest years 1995–1997) and at Parlier, CA (harvest years 1998–2004) on a Hanford loam soil with drip irrigation (Tables 1 and 2). In both locations, plant stands were established from transplants (60–72 plants/accession) that were planted in the field under isolation cages (3.5 m × 3.5 m × 1.8 m, 20 × 20 polyethylene mesh screen) to prevent cross pollination. Blue bottle flies (*Protophormia terraenovae* Robineau-Devoidy) were used as pollinators. Harvested plant material was dried in a shed with air circulated by fans (25–32 °C) for two weeks and after, the dry material was threshed using a custom made small belt thresher. Seeds were pre-cleaned in a seed blower (Seedburo) and fine cleaned by hand. Until analysis, seeds were stored at 4 °C and 20% RH in paper bags.

Seed color was evaluated visually after dry seeds were threshed and cleaned. Fatty-acid content (%), i.e. palmitic, palmitoleic, stearic, total oleic, linolenic, linoleic, arachidic, ricinoleic, densipolic, lesquerolic, and auricolic in the seeds was measured by gas chromatography in four replicates (0.5 g/replicate). However, 42 accessions were analyzed in five replicates and 20 in only three replicates. All material was analyzed at the same time.

Fatty acid methyl esters were synthesized by placing 50 seeds in a 25 mL screw cap vial and 4 mL of 0.25 M sodium methoxide was added. The seeds were thoroughly ground in the sodium methoxide solution by a tissue homogenizer (Cole Parmer, Vernon Hills, IL) with a 10 mm coarse generator for approximately 60 s until no whole seeds were visible. An aluminum lined cap was placed on the vial and the vial placed in a heating block maintained at 60 °C. After 30 min, the vial was removed from the heating block and allowed to cool to near room temperature. Saturated sodium chloride solution (2 mL) and 4 mL of hexane were added to the vial. The cap was placed on the vial and the contents shaken thoroughly. The vial was allowed to stand for 5 min and 2 mL of the top hexane layer containing the methyl esters was removed and placed in a GC target vial and analyzed using the conditions described below.

Gas chromatography (GC) was performed with a Hewlett-Packard 6890 N gas chromatograph (Palo Alto, CA), equipped with a flame-ionization detector and an autosampler/injector. Analyses were conducted on a SP 2380 30 m × 0.25 mm i.d. × 0.2 μm film thickness (Supelco, Bellefonte, PA) column. Saturated C_8–C_{30} FAMEs standards obtained from Nu-Check Prep Inc. (Elysian, MN) provided standards to make fatty-acid methyl ester assignments. SP 2380 analysis were conducted as follows: total flow 15 mL/min with helium head pressure of 172 kPa (25 psi) with a split flow of 10.7 mL/min to give a split ratio of 6.9:1; programmed ramp 180–210 °C at 7 °C/min, 210–265 °C at 30 °C/min; hold 5 min at 265 °C; injector and detector temperatures set at 265 °C. Injection of volume of 5 μL was used.

Data were evaluated by ANOVA (Tukey-Kramer HSD, $\alpha = 0.05$, JMP, version 7; SAS). Standard error was calculated across all accessions and species. Since none of the accessions were grown in the same location or the same year, but the data were confounded by accession, the analysis was treated conservatively by nesting the accessions within locations and analyzing the data as a mixed model where an accession was a variable (random sample) and the location (Parlier, CA and Pullman, WA) or harvest year (1995, 1996, 1997, 1998, 1999, 2000, 2002, 2003, and 2004) were fixed effects (Fit-model method, α 0.05, JMP, version 7, SAS). The Fit-model analysis was carried out only for species with the largest number of accessions, such as *L. argyraea*, *L. fendleri*, and *L. gordonii* (11, 104, and 17 accessions, respectively).

Table 1 – Average content (%) of fatty acids in non-*fendleri Lesquerella* species and accessions maintained by the NPGS collection

ID	Number	Species	Harvest year	Location[d]	Seed color[e]	Fatty acid										
						Palmitic	Palmitoleic	Stearic	Oleic	Linolenic	Linoleic	Arachidic	Ricinoleic	Densipolic	Lesquerolic	Auricolic
W6	20813	*L. angustifolia*	2004	CA	DB	1.8	0.9	1.1	11.0	8.3	2.7	0.2	3.8	0.0	67.4	0.2
W6	20814	*L. angustifolia*	2004	CA	DB	1.6	0.7	0.9	12.2	8.0	2.6	0.2	4.1	0.0	66.4	0.3
PI	344035	*L. angustifolia*	2002	CA	BN	1.5	0.9	1.2	12.2	7.4	2.6	0.1	4.7	0.1	67.9	0.2
PI	355033	*L. angustifolia*	2003	CA	BN	3.4	2.8	1.7	17.6	11.3	5.7	0.0	2.4	0.0	53.2	0.0
		Mean ± S.E.[a]				2.1 ± 0.2	1.3 ± 0.2	1.2 ± 0.1	13.0 ± 0.7	8.7 ± 0.4	3.3 ±± 0.4	0.1 ± 0.0	3.8 + 0.3	0.0	64.2 ±± 0.3	0.2 + 0.1
W6	20815	*L. argyraea*	2004	CA	BN	1.2	0.5	1.7	12.2	8.1	6.6	0.3	0.4	0.0	64.3	1.1
W6	20816	*L. argyraea*	2004	CA	BE	1.4	0.5	1.8	14.0	7.4	7.3	0.5	0.4	0.0	62.0	1.0
W6	20863	*L. argyraea*	1999	CA	BE	2.3	1.0	1.6	15.8	10.7	9.5	0.4	0.0	0.0	55.3	0.6
W6	20864	*L. argyraea*	1999	CA	DB	1.5	1.3	1.3	8.9	7.6	6.2	0.2	0.1	0.0	71.3	0.0
W6	20866	*L. argyraea*	1999	CA	BN	1.4	0.5	1.8	13.7	9.0	7.0	0.1	0.2	0.1	64.5	0.8
W6	20867	*L. argyraea*	1999	CA	BE	1.7	0.8	1.7	13.1	8.3	7.8	0.2	0.4	0.0	63.6	1.2
PI	596449	*L. argyraea*	1996	WA	BE	1.2	0.7	1.3	12.8	5.7	10.2	0.4	0.8	0.0	61.0	3.8
PI	596451	*L. argyraea*	1996	WA	BE	1.2	0.7	1.3	12.6	5.9	10.8	0.3	0.8	0.0	60.0	4.0
PI	641921	*L. argyraea*	2003	CA	BE	1.2	0.4	1.8	11.2	6.4	10.7	0.1	0.4	0.0	63.9	2.4
PI	643169	*L. argyraea*	2003	CA	BN	1.9	1.7	0.7	20.6	6.6	12.3	0.1	0.3	0.1	53.0	1.2
PI	643178	*L. argyraea*	2003	CA	YW	1.5	0.8	2.4	14.3	6.2	13.6	0.0	0.1	0.0	56.7	2.9
		Mean ± S.E.				1.5 ± 0.1	0.8 ± 0.1	1.6 ± 0.1	13.6 ± 0.5	7.4 ± 0.2	9.3 ± 0.4	0.2 ± 0.1	0.4 ± 0.1	0.0	61.4 ± 0.9	1.7 ± 0.2
W6	20827	*L. arizonica*	2004	CA	BN	1.7 ± 0.1	0.6 ± 0.3	1.3 ± 0.1	15.8 ± 0.8	5.7 ± 0.2	10.9 ± 0.2	0.1 ± 0.1	1.0 ± 0.0	0.3 ± 0.0	57.3 ± 1.9	3.2 ± 0.1
W6	20319	*L. auriculata*	1999	CA	DB	3.2	0.8	3.6	20.5	0.8	10.2	0.2	3.9	1.7	11.3	40.7
W6	20320	*L. auriculata*	1999	CA	DB	3.4	0.9	4.2	17.9	2.0	11.7	0.6	3.9	2.4	9.3	39.3
PI	345712	*L. auriculata*	1997	WA	DB	3.2	1.1	4.4	21.2	1.0	8.3	0.3	4.3	2.6	12.9	38.3
		Mean ± S.E.				3.3 ± 0.1	0.9 ± 0.1	4.0 ± 0.3	19.8 ± 0.6	1.3 ± 0.3	10.2 ± 0.5	0.4 ± 0.1	4.2 ± 0.2	2.2 ± 0.2	11.0 ± 0.6	39.5 ± 0.9
W6	20818	*L. cinerea*	1999	CA	BE	1.8 ± 0.0	1.0 ± 0.4	1.3 ± 0.0	16.5 ± 0.2	11.4 ± 0.2	5.0 ± 0.1	0.2 ± 0.1	0.8 ± 0.0	0.0	59.7 ± 0.5	0.5 ± 0.0
W6	20819	*L. densiflora*	2004	CA	DB	3.6 ± 0.1	1.1 ± 0.4	4.9 ± 0.2	22.5 ± 0.5	1.8 ± 0.5	8.3 ± 0.1	0.5 ± 0.1	4.8 ± 0.3	2.0 ± 0.1	12.7 ± 0.3	33.9 ± 1.2
PI	292577	*L. densipila*	2000	CA	BE	4.1	0.8	3.7	19.0	0.7	10.7	0.3	10.0	46.4	1.7	0.0
PI	309661	*L. densipila*	2003	CA	DB	4.1	1.1	4.0	21.7	0.9	10.7	0.4	12.3	41.0	1.1	0.0
PI	315051	*L. densipila*	2003	CA	DB	3.9	0.6	4.5	22.9	1.2	9.9	0.4	12.0	42.6	0.0	0.0
PI	355035	*L. densipila*	2003	CA	DB	3.8	0.9	4.1	20.0	1.1	10.1	0.3	10.4	46.8	0.6	0.0
		Mean ± S.E.				4.0 ± 0.1	0.9 ± 0.1	4.1 ± 0.1	20.9 ± 0.6	1.0 ± 0.2	10.4 ± 0.2	0.4 ± 0.1	11.2 ± 0.4	44.2 ± 3.2	0.9 ± 0.3	0.0
W6	20820	*L. douglasii*	2004	CA	DB	1.5	1.1	0.7	14.2	6.0	13.5	0.2	3.4	1.1	52.1	3.1
W6	23377	*L. douglasii*	1999	CA	BE	1.8	1.8	0.5	11.2	7.6	15.3	0.2	2.6	0.4	52.5	2.0
		Mean ± S.E.				1.6 ± 0.1	1.4 ± 0.2	0.6 ± 0.1	12.7 ± 1.4	6.8 ± 0.3	14.4 ± 0.4	0.2 ± 0.1	3.0 ± 0.5	0.7 ± 0.5	52.3 ± 0.9	2.5 ± 0.4
W6	20832	*L. gordonii*	2004	CA	DB	1.2	0.6	1.3	14.4	3.8	6.0	0.1	0.6	0.0	67.7	2.5
W6	20833	*L. gordonii*	2004	CA	DB	1.3	1.3	1.3	14.4	4.0	5.4	1.7	0.4	0.0	65.6	2.5
W6	23373	*L. gordonii*	1999	CA	BN	1.5	1.4	0.9	14.6	4.4	7.2	0.2	0.3	0.0	65.4	1.8
W6	23374	*L. gordonii*	2004	CA	BE	1.4	0.9	1.4	11.3	6.0	14.3	0.3	0.3	0.1	57.9	3.1
W6	23383	*L. gordonii*	2004	CA	BN	1.4	1.4	1.0	15.9	4.2	7.3	0.1	0.6	0.0	64.1	2.4
PI	293017	*L. gordonii*	1997	WA	DB	1.3	1.0	1.5	15.1	3.8	6.6	0.1	0.7	0.1	66.5	2.3
PI	293018	*L. gordonii*	2003	CA	BN	1.7	1.7	1.4	16.9	5.9	5.3	0.0	0.5	0.0	64.4	1.1
PI	293019	*L. gordonii*	uni[c]	WA	BN	1.7	1.7	1.5	18.3	5.8	5.0	0.0	0.3	0.0	63.1	1.5
PI	293020	*L. gordonii*	2004	CA	BN	1.5	1.4	1.5	14.9	4.7	5.7	0.0	0.4	0.0	67.9	1.6
PI	293029	*L. gordonii*	1999	CA	BN	1.3	1.1	1.4	17.1	4.3	6.7	0.0	0.3	0.0	64.7	2.6
PI	293030	*L. gordonii*	2004	CA	DB	1.5	1.3	1.4	14.9	3.5	7.0	0.0	0.6	0.0	65.8	3.3
PI	293031	*L. gordonii*	1999	CA	BE	1.5	0.4	1.7	13.2	9.2	6.6	0.0	0.4	0.0	65.8	0.8
PI	299142	*L. gordonii*	2000	CA	DB	1.7	1.9	1.8	17.1	5.4	7.8	0.0	0.0	0.0	61.3	2.2
PI	306127	*L. gordonii*	2004	CA	DB	2.1	1.3	2.2	19.3	6.3	8.0	0.0	0.2	0.0	58.1	1.3
PI	306128	*L. gordonii*	1999	CA	BN	2.3	1.8	2.5	18.7	6.5	7.7	0.0	0.3	0.0	57.0	1.7
PI	330629	*L. gordonii*	2004	CA	DB	1.5	1.4	1.3	16.6	5.5	5.5	0.0	0.6	0.2	65.4	1.3
PI	330630	*L. gordonii*	2004	CA	DB	1.9	1.7	1.7	20.0	5.5	5.9	0.2	0.6	0.0	59.4	1.7
		Mean ± S.E.				1.6 ± 0.0	1.3 ± 0.1	1.5 ± 0.1	15.9 ± 0.3	5.2 ± 0.2	6.9 ± 0.3	0.2 ± 0.1	0.4 ± 0.0	0.0	63.9 ± 0.5	2.0 ± 0.1
W6	20834	*L. gracilis*	2004	CA	DB	1.5	1.0	1.1	17.3	4.6	4.9	1.7	0.5	0.0	63.9	1.8
W6	23380	*L. gracilis*	1999	CA	BN	1.9	1.4	0.6	12.4	8.6	3.5	0.1	3.1	0.2	65.6	0.1

		Mean ± S.E.				1.7 ± 0.1	1.2 ± 0.1	0.9 ± 0.1	14.9 ± 0.9	6.6 ± 0.8	4.2 ± 0.7	0.9 ± 0.8	0.4 ± 0.0	0.0	63.9 ± 0.5	2.0 ± 0.1
W6	20835	*L. grandiflora*	2004	CA	DB	1.3	0.6	3.8	22.8	6.4	1.5	0.1	2.5	0.1	58.0	0.1
W6	20836	*L. grandiflora*	2004	CA	DB	1.3	0.6	3.5	21.2	5.6	1.5	0.2	2.4	0.1	60.3	0.2
W6	20837	*L. grandiflora*	1998	CA	DB	1.0	0.7	3.4	21.1	5.2	1.7	0.2	2.5	0.1	59.8	0.3
PI	293033	*L. grandiflora*	2000	CA	BN	1.2	0.6	3.7	20.5	6.5	1.4	0.1	2.2	0.0	61.6	0.1
PI	293034	*L. grandiflora*	2000	CA	BN	1.3	0.9	3.6	20.4	6.7	1.4	0.1	2.2	0.0	61.4	0.0
		Mean ± S.E.				1.2 ± 0.0	0.7 ± 0.1	3.6 ± 0.1	21.2 ± 0.3	6.1 ± 0.2	1.5 ± 0.0	0.1 ± 0.0	2.4 ± 0.2	0.0	60.2 ± 0.8	0.1 ± 0.0
W6	20838	*L. intermedia*	1998	CA	BE	1.9	0.9	1.2	20.2	6.2	11.7	0.0	0.9	0.1	52.7	2.9
W6	20839	*L. intermedia*	2004	CA	BN	1.9	1.4	1.1	12.9	5.4	13.0	0.0	0.8	0.1	57.9	3.7
W6	23375	*L. intermedia*	2004	CA	BE	2.1	2.0	0.8	15.0	7.5	10.5	0.1	0.3	0.1	58.9	1.0
W6	23376	*L. intermedia*	2004	CA	DB	1.4	1.1	1.5	11.1	6.6	13.4	0.1	0.5	0.1	58.6	3.1
		Mean ± S.E.				1.8 ± 0.1	1.4 ± 0.1	1.2 ± 0.1	14.8 ± 1.4	6.4 ± 0.2	12.2 ± 0.3	0.1 ± 0.0	0.6 ± 0.1	0.1 ± 0.0	57.0 ± 1.1	2.7 ± 0.4
PI	293036	*L. lasiocarpa*	2000	CA	DB	1.6	1.2	3.0	20.2	4.6	2.6	0.2	1.9	0.0	61.4	0.7
PI	643172	*L. lasiocarpa*	2004	CA	DB	1.2	0.8	3.9	23.8	5.8	2.1	0.0	1.2	0.1	59.3	0.1
PI	643173	*L. lasiocarpa*	2003	CA	DB	1.3	0.7	2.9	21.2	4.9	2.2	0.0	1.8	0.1	61.8	0.1
		Mean ± S.E.				1.4 ± 0.1	0.9 ± 0.2	3.2 ± 0.3	21.7 ± 1.1	5.1 ± 0.3	2.3 ± 0.2	0.1 ± 0.0	1.6 ± 0.3	0.0	60.8 ± 1.1	0.3 ± 0.1
PI	315053	*L. lescurii*	2000	CA	DB	4.5 ± 0.1	1.2 ± 0.0	4.0 ± 0.1	20.5 ± 0.8	0.9 ± 0.5	12.0 ± 0.2	0.4 ± 0.2	10.9 ± 0.6	43.3 ± 1.4	0.0	0.0
PI	643174	*L. lindheimeri*	2004	CA	BN	1.1 ± 0.1	0.3 ± 0.1	1.9 ± 0.1	6.7 ± 0.3	3.7 ± 0.1	1.1 ± 0.0	01 ± 0.1	0.7 ± 0.2	0.0	82.8 ± 1.3	0.0
PI	355046	*L. ludoviciana*	2003	CA	BN	1.6 ± 0.2	1.4 ± 0.1	0.3 ± 0.2	15.0 ± 1.6	2.6 ± 1.2	18.7 ± 1.4	0.0	9.1 ± 4.3	14.0 ± 0.4	30.2 ± 0.5	6.2 ± 0.1
PI	275769	*L. lyrata*	1999	CA	DB	4.1 ± 0.2	0.9 ± 0.0	4.4 ± 0.2	21.4 ± 1.0	1.2 ± 0.6	10.0 ± 0.6	0.4 ± 0.1	10.8 ± 05	43.4 ± 1.4	0.7 ± 0.7	0.0
W6	20844	*L. mcvaughiana*	1997	WA	BN	1.6 ± 0.1	1.0 ± 0.0	1.6 ± 0.0	15.2 ± 0.2	7.9 ± 0.3	8.9 ± 0.2	01 ± 0.1	0.5 ± 0.2	0.1 ± 0.1	59.2 ± 0.9	2.0 ± 0.1
PI	643175	*L. mexicana*	2003	CA	BN	1.6 ± 0.1	1.3 ± 0.1	2.1 ± 0.1	12.3 ± 3.8	9.7 ± 0.5	7.3 ± 0.4	0.1 ± 0.1	0.6 ± 0.2	01 ± 0.1	62.1 ± 4.4	1.1 ± 0.4
W6	23384	*L. montana*	1999	CA	BN	1.7 ± 0.1	1.8 ± 0.1	0.8 ± 02	13.5 ± 3.6	5.6 ± 0.2	14.6 ± 0.6	0.1 ± 0.1	0.8 ± 0.1	01 ± 0.1	56.2 ± 2.8	3.0 ± 1.0
W6	20845	*L. multiceps*	2004	CA	BN	1.3 ± 0.0	0.9 ± 0.1	1.6 ± 0.1	14.2 ± 0.4	6.0 ± 0.2	12.9 ± 0.3	0.0	0.6 ± 0.0	0.0	56.9 ± 0.7	3.9 ± 0.1
W6	20846	*L. ovalifolia*	1997	WA	BE	1.7	1.2	1.3	13.6	7.1	13.9	0.0	0.8	0.1	55.8	3.5
W6	23378	*L. ovalifolia*	2004	CA	DB	1.2	0.8	0.5	13.0	9.9	11.0	0.1	0.4	0.1	59.9	1.1
W6	23379	*L. ovalifolia*	2004	CA	BN	2.5	2.6	1.0	9.0	10.4	14.8	0.4	0.5	0.2	54.5	1.0
W6	23381	*L. ovalifolia*	1999	CA	BN	1.8	1.6	0.8	11.6	7.2	14.0	0.2	0.5	0.2	55.2	3.9
W6	23382	*L. ovalifolia*	1999	CA	BN	1.5	1.3	0.8	8.0	8.4	12.4	0.1	0.7	0.1	61.3	2.2
		Mean ± S.E.				1.7 ± 0.1	1.5 ± 0.2	0.9 ± 0.1	11.2 ± 1.1	8.5 ± 0.4	13.3 ± 0.4	0.2 ± 0.1	0.6 ± 0.1	0.1 ± 0.1	57.0 ± 1.1	2.4 ± 0.4
W6	20847	*L. pallida*	2004	CA	DB	1.1 ± 0.1	0.5 ± 0.0	0.6 ± 0.2	3.1 ± 0.6	3.6 ± 0.1	2.7 ± 0.1	0.1 ± 0.1	1.7 ± 0.6	0.0	84.6 ± 0.7	0.1 ± 0.1
PI	306129	*L. palmeri*	2003	CA	BN	2.3	2.0	2.2	21.1	6.7	6.9	0.0	0.4	0.0	56.1	1.0
PI	307830	*L. palmeri*	1999	CA	DB	2.4	2.0	2.3	20.9	6.9	6.7	0.1	0.4	0.0	55.9	1.3
PI	330631	*L. palmeri*	2000	CA	BN	1.6	1.6	1.5	18.1	4.7	6.1	0.1	0.6	0.0	62.5	2.0
		Mean ± S.E.				2.1 ± 0.2	1.9 ± 0.0	2.0 ± 0.2	20.0 ± 0.9	6.1 ± 0.6	6.6 ± 0.2	0.1 ± 0.1	0.5 ± 0.2	0.0	58.2 ± 2.1	1.5 ± 0.4
PI	275770	*L. perforata*	2000	CA	DB	4.6	1.0	3.3	18.1	1.5	11.3	0.2	11.6	45.4	0.0	0.0
PI	355041	*L. perforata*	2003	CA	DB	3.9	0.9	4.1	20.0	1.0	10.4	0.3	9.6	47.1	0.8	0.0
		Mean ± S.E.				4.3 ± 0.2	1.0 ± 0.0	3.7 ± 0.2	19.1 ± 0.8	1.3 ± 0.2	10.9 ± 0.3	0.3 ± 0.1	10.6 ± 0.5	46.2 ± 1.3	0.4 ± 0.4	0.0
W6	20848	*L. pinetorum*	1999	CA	DB	1.6	1.0	1.4	16.9	10.1	4.9	0.1	0.6	0.1	59.4	0.6
PI	293037	*L. pinetorum*	2004	CA	DB	2.0	2.4	1.4	17.8	9.8	6.4	0.1	0.8	0.0	57.7	0.6
		Mean ± S.E.				1.7 ± 0.1	1.5 ± 0.3	1.4 ± 0.0	17.2 ± 0.3	10.1 ± 0.1	5.4 ± 0.3	0.1 ± 0.0	0.6 ± 0.1	0.1 ± 0.1	58.8 ± 0.6	0.6 ± 0.1
W6	20817	*L. rectipes*	2004	CA	BN	1.6	1.1	0.9	13.3	7.3	11.3	0.2	0.7	0.0	59.3	2.0
W6	20849	*L. rectipes*	1999	CA	BE	1.8	2.1	0.8	11.2	6.1	13.1	0.1	0.5	0.1	56.9	2.1
W6	20850	*L. rectipes*	2004	CA	BN	1.4	1.3	1.5	14.9	4.7	6.3	0.1	0.3	0.1	66.0	1.7
W6	20851	*L. rectipes*	2004	CA	BE	1.7	1.6	1.0	17.8	5.4	12.6	0.1	0.9	0.1	54.5	2.0
W6	20852	*L. rectipes*	2004	CA	BE	2.0	1.7	0.5	16.0	7.2	12.4	0.1	0.4	0.1	56.7	1.1
		Mean ± S.E.				1.7 ± 0.0	1.6 ± 0.1	1.0 ± 0.1	14.6 ± 0.8	6.2 ± 0.4	11.2 ± 0.6	0.1 ± 0.0	0.6 ± 0.1	0.1 ± 0.0	58.7 ± 1.1	1.8 ± 0.3
PI	643180	*L. schaffneri*	2003	CA	BE	1.0 ± 0.1	0.6 ± 0.1	2.6 ± 0.1	12.3 ± 0.6	9.4 ± 0.2	8.3 ± 0.2	0.0	0.3 ± 0.1	0.0	64.1 ± 1.2	1.1 ± 0.1
W6	23385	*L.* sp.[b]	1999	CA	BN	1.7	1.8	0.6	18.9	9.0	11.9	0.1	4.8	0.6	45.0	1.2
PI	302490	*L.* sp.	2003	CA	BN	2.3	1.9	2.3	20.3	6.5	6.1	0.0	0.2	0.0	58.2	1.5
		Mean ± S.E.				2.0 ± 0.1	1.9 ± 0.1	1.4 ± 0.3	19.6 ± 0.5	7.7 ± 0.5	9.0 ± 1.1	0.0	2.5 ± 1.2	0.3 ± 0.2	51.6 ± 2.6	1.4 ± 0.2
PI	275771	*L. stonensis*	2003	CA	DB	4.1	0.8	4.1	19.7	0.5	10.3	0.3	9.6	47.2	0.0	0.0

Table 1 – (Continued)

ID	Number	Species	Harvest year	Location[d]	Seed color[e]	Fatty acid										
						Palmitic	Palmitoleic	Stearic	Oleic	Linolenic	Linoleic	Arachidic	Ricinoleic	Densipolic	Lesquerolic	Auricolic
PI	355042	*L. stonensis*	2003	CA	DB	4.7	1.1	4.5	21.7	0.8	11.5	0.4	8.4	45.0	0.0	0.0
		Mean ± S.E.				4.4 ± 0.2	1.0 ± 0.1	4.3 ± 0.2	20.7 ± 0.9	0.7 ± 0.2	10.9 ± 0.4	0.4 ± 0.1	9.0 ± 0.5	46.1 ± 1.1	0.0	0.0
PARL	164	*L. wardii*	2003	CA	BN	1.8	0.8	0.8	17.1	7.9	13.2	0.0	0.4	0.1	54.7	1.8
PARL	165	*L. wardii*	2003	CA	BN	1.2	0.7	0.8	18.1	8.8	13.2	0.0	0.0	0.0	55.2	1.1
		Mean ± S.E.				1.5 ± 0.2	0.7 ± 0.3	0.8 ± 0.3	17.6 ± 1.1	8.4 ± 0.4	13.2 ± 0.7	0.0	0.2 ± 0.1	0.0	54.9 ± 1.1	1.4 ± 0.6

[a] S.E. – standard error.
[b] sp. – species not identified.
[c] uni – harvest year not known.
[d] CA – California; WA – Washington.
[e] BE – beige; BN – brown; DB – dark brown; YW – yellow.

3. Results

3.1. Variation in fatty acids among species

The average content (%) of the four HFA in seeds varied among the 32 *Lesquerella* species (Tables 1 and 2). In this study, the most abundant HFA found in seeds of the 195 accessions was lesquerolic acid (average of over 80.0% in *L. pallida* and *L. lindheimeri*). Densipolic acid was the prevalent HFA in the species from the eastern U.S. (average of over 40.0% in *L. perforata*, *L. stonensis*, *L. densipila*, *L. lyrata*, and *L. lescurii*). Auricolic acid was the prevalent HFA in two species (average of over 30.0% in *L. auriculata* and *L. densiflora*) and ricinoleic acid of >10.0% was observed in *L. densipila*, *L. lescurii*, *L. lyrata* and *L. perforata*. The highest content of oleic acid, which is a precursor to three of the HFAs (lesquerolic, densipolic and auricolic) (Reed et al., 1997; Broun et al., 1998), was found in *L. densiflora*, *L. lasiocarpa*, *L. lyrata*, *L. grandiflora*, *L. densipila*, *L. stonensis*, *L. lescurii*, and *L. palmeri* (average of over 20.0%). The highest content of linoleic acid was in *L. ludoviciana* (average of 18.7%). The average content of the other five fatty acids analyzed in this study was below 12.0%; i.e., linolenic 11.4% in *L. cinerea*; stearic >4.0% in *L. densiflora*, *L. lyrata*, *L. stonensis*, *L. densipila*, *L. auriculata*, *L. lescurii*; palmitic >4.0% in *L. lescurii*, *L. stonensis*, *L. perforata*, and *L. lyrata*. Low content of palmitoleic acid (from 0.3 to 1.9%) was observed in all 32 *Lesquerella* species, with traces of arachidic (0–0.9%) in 29 *Lesquerella* species. The range of the fatty-acid content also varied among species (Tables 1 and 2). For species with five or more accessions, the range of the most abundant HFA in the *Lesquerella* genus – lesquerolic HFA was 53.0–71.3% for *L. argyraea* (11 accessions), 43.3–66.3% for *L. fendleri* (104 accessions), 57.0–67.9% for *L. gordonii* (17 accessions), 0–0.3% for *L. grandiflora* (5 accessions), 54.5–61.3 % for *L. ovalifolia* (5 accessions), and 54.5–66.0% for *L. rectipes* (5 accessions) (Table 1). The largest difference in the content of the acids analyzed was observed for densipolic HFA (0% in *L. argyraea*, 46.2% in *L. perforata*).

3.2. Variation of fatty acids among accessions

The content (%) of the four HFA (lesquerolic, densipolic, auricolic and ricinoleic) and the seven other fatty acids varied among accessions of the same species and across the 195 accessions (Tables 1 and 2). Species with the highest content of lesquerolic acid (*L. pallida* and *L. lindheimeri*) were represented only with one accession each (W6 20847, 84.6 and PI 643174, 82.8%, respectively; Table 1).

In *L. fendleri* (104 accessions) the highest content of the HFA was in seeds of accession W6 20829 (66.3%; Table 2); however, the content of lesquerolic acid was not different in 101 other accessions of the species. This accession (W6 20829) had also one of the lowest values of unsaturated (linolenic and linoleic) fatty acids. In *L. gordonii* (17 accessions), the highest content of lesquerolic acid was in PI 293020 and W6 20832 (both >67%), but this level was not significantly different from the level in 10 other accessions of this species. In *L. argyraea* (11 accessions), the highest content of lesquerolic acid was in W6 20864 (71.3%) which was not significantly different from the content in the four other accessions of the species. Traces of lesquerolic acid were observed in three species (*L. densipila*, *L. lyrata* and *L. perforata*; 0.9, 0.7 and 0.4%, respectively); and in two species, *L. lescurii* and *L. stonensis*, no lesquerolic acid was found.

The content of densipolic acid was low in all accessions of *L. fendleri*, *L. argyraea* and *L. gordonii* (0–3.1% in PI 293005; Tables 1 and 2). The highest content of densipolic acid was in PI 275771 (*L. stonensis*, 47.2%), PI 355041 (*L. perforata*, 47.1%), PI 355035 (*L. densipila*, 46.8%), PI 295577 (*L. densipila*, 46.4%), and PI 275770 (*L. perforata*, 45.4%); the level of densipolic acid was not significantly different in the five accessions. A high densipolic acid content was also observed in five other accessions: PI 355042 (*L. stonensis*, 45.0%), PI 275769 (*L. lyrata*, 43.4%), PI 315053 (*L. lescurii*, 43.3%); PI 315051 and PI 309661 (*L. densipila*, 42.6% and 41.0%, respectively). The content of densipolic acid was significantly lower in all other accessions.

Two accessions, W6 20319 and W6 20320 (both *L. auriculata*), had significantly higher contents of auricolic acid (40.7% and 39.3%, respectively) than the other 193 accessions. In *L. fendleri*, the highest content of auricolic acid was in PI 299412 (6.2%); however, this level was not significantly different from the content in 96 other *L. fendleri* accessions. In *L. argyraea*, the highest content of auricolic acid was in PI 596451 and PI 596449 (4.0 and 3.3%, respectively); however, these levels were not significantly different from two other accessions (PI 643178 and PI 641921). In *L. gordonii*, the level of auricolic acid was similar in all 17 accessions.

The highest content of oleic acid was in PI 643172 (*L. lasiocarpa*, 23.8%) but statistically, 55 other accessions had a similar content. In *L. fendleri*, 99 out of the 104 accessions analyzed had no significant difference in oleic acid content, with the highest in PI 643171 (18.5%). PI 643169 had significantly higher content of oleic acid in *L. argyraea* (20.6%) than the other 10 accessions. In *L. gordonii*, the accession with the highest oleic content (PI 330630, 20.0%) was not significantly different from 13 other accessions.

Linoleic acid was most abundant in PI 355046 (*L. ludoviciana*, 18.7%), and only six other accessions (W6 23377 *L. douglasii*, three accessions of *L. fendleri* W6 20859, W6 20862 and PI 279650, W6 23379 *L. ovalifolia*, and W6 23384 *L. montana*) had similar contents. Of the *L. fendleri* accessions, W6 20862 had the highest content of linoleic acid (15.3%), but this content was not significantly different from 82 other accessions of this species. In *L. argyraea*, two accessions (PI 643178 and 643169) had similar linolenic acid contents (13.7 and 12.3%, respectively). W6 23374 (*L. gordonii*, 14.3%) had significantly higher linoleic acid content than the 16 other accessions of this species. The lowest linoleic value was in accessions PI 293033 and PI 293034 (both *L. grandiflora*).

The highest content of linolenic acid was in W6 20818 (*L. cinerea*, 11.4%) but this component was not significantly different from 14 other accessions. In *L. fendleri*, the highest content was in W6 20873 (8.2%) but no significant difference was found compared to 80 other accessions of the species. W6 20863 had significantly higher linolenic acid content than did the other 10 accessions of *L. argyraea*. In *L. gordonii*, significantly higher content of linolenic acid was found in PI 293031 (9.2%) than in the other *L. gordonii* accessions.

Ricinoleic acid, a precursor to densipolic acid, was most abundant in PI 309661 (*L. densipila*, 12.3%); and this level was similar to only six other accessions (the three remaining accessions of *L. densipila* PI 293577, PI 315051 and PI 355035, *L. perforata* PI 275770 and PI 355041, *L. lescurii* PI 315053, and *L. lyrata* PI 275769). In *L. fendleri*, the highest ricinoleic acid content was in W6 20862 (1.5%), but in 70 other accessions of this species, levels were not significantly different. In *L. argyraea*, the ricinoleic acid content was not significantly different in all nine accessions, with the highest content in PI 596449 (0.8%). Among *L. gordonii* accessions, the highest content of ricinoleic acid was in PI 293017 (0.6%), and this level was not significantly different from 15 other accessions of the species; however, no ricinoleic acid was observed in PI 299142.

Stearic acid content was the highest in W6 20819 (*L. densiflora*, 4.9%), and this level was similar to that of 16 other accessions. In species with the largest number of accessions, *L. fendleri*, *L. argyraea* and *L. gordonii*, accessions with the highest stearic acid content were PI 643179 (2.1%), PI 643178 (2.4%) and PI 643178 (2.4%), respectively.

Palmitic acid levels were the highest in PI 355042 (*L. stonensis*, 4.7%); and this level was not significantly different to that of nine other accessions: PI 275770 and PI 355041 (*L. perforata*), PI 315053 (*L. lescurii*), PI 292577, PI 309661, PI 315051 and PI 355035 (*L. densipila*), PI 275771 (*L. stonensis*), and PI 275769 (*L. lyrata*). In *L. fendleri*, the content of palmitic acid was similar in 98 accessions, with the highest in PI 641918 (1.9%). In *L. argyraea*, W6 20863 had significantly higher content of palmitic acid (2.3%) than the other 10 *L. argyraea* accessions. In *L. gordonii*, significantly higher palmitic acid content was found in PI 306128 and PI 306127 than in the 15 other accessions.

Seeds of PI 355033 (*L. angustifolia*) contained the highest palmitoleic acid (2.8%); yet this level was not significantly different from the levels in 20 other accessions in the *Lesquerella* collection. In *L. fendleri*, three accessions, PI 596437, PI 596435 and PI 596441, had significantly higher content of palmitoleic acid than did the other 101 accessions of this species. In *L. argyraea*, the highest palmitoleic acid was in PI 643169 (1.7%), and this level was similar to those of three other accessions (W6 20864, W6 20863 and W6 20867) of this species. PI 299142 had the highest content of palmitoleic acid (1.9%) in *L. gordonii*; however, this level was not significantly different from the content in seeds of 12 other accessions of this species.

Out of the 195 accessions, the highest content of arachidic acid was in W6 20833 (1.7%, *L. gordonii*). Only 68 accessions of *L. fendleri* contained traces of arachidic acid (0.04–0.6%, PI 596428 and PI 596437, respectively). Seeds of all other accessions did not contain this fatty acid. Nine of 11 accessions of *L. argyraea* contained arachidic acid, with the highest content in W6 20816 (0.5%). In *L. gordonii*, arachidic acid was in eight of the 17 accessions evaluated; the highest content was in W6 20833 (1.7%).

3.3. *Influence of location, year of harvest, and seed color*

Content of a particular fatty acid was influenced by the location, harvest year and the seed color (Table 3). In *L. fendleri*, the content of lesquerolic, linoleic, linolenic and arachidic acids in seeds harvested in California was significantly higher than in seeds grown in Washington. Seed harvested in 1999, 2000 and 2003 yielded a significantly higher content of lesquerolic acid than seeds harvested in 1995. In *L. fendleri*, the content of den-

Table 2 – Average content (%) of fatty acids in *L. fendleri* accessions maintained in the NPGS germplasm collection

ID	Number	Harvest year	Location	Seed color	Fatty acid										
					Palmitic	Palmitoleic	Stearic	Oleic	Linolenic	Linoleic	Arachidic	Ricinoleic	Densipolic	Lesquerolic	Auricolic
W6	20822	1997	WA	BE	1.3	0.7	1.6	13.8	6.9	11.0	0.2	0.9	0.0	58.1	3.4
W6	20823	1997	WA	BE	1.3	0.8	1.5	13.0	6.1	11.3	0.4	0.9	0.0	58.1	4.1
W6	20824	1997	WA	BE	1.2	0.4	1.5	13.0	5.9	10.9	0.1	0.9	0.0	60.1	3.8
W6	20825	1998	WA	BE	1.4	0.5	1.6	13.1	6.8	10.7	0.3	0.8	0.0	58.7	3.4
W6	20826	1998	CA	BE	1.4	0.5	1.8	14.7	5.9	10.6	0.4	0.9	0.0	56.7	4.1
W6	20829	2004	CA	BN	1.4	0.6	1.3	14.3	4.3	6.4	0.2	0.6	0.0	66.3	2.8
W6	20830	1997	CA	BE	1.4	0.4	1.5	13.1	6.0	11.3	0.2	0.8	0.0	59.3	3.9
W6	20831	1998	CA	BE	1.4	0.7	1.6	14.3	5.9	10.1	0.4	0.3	0.0	57.5	3.4
W6	20856	2004	CA	BE	1.0	0.7	0.9	15.2	4.9	12.6	0.2	0.5	0.0	57.4	3.8
W6	20857	1997	WA	BE	1.4	0.6	1.3	14.5	6.5	11.2	0.1	0.6	0.0	58.1	3.1
W6	20858	2004	CA	BN	1.4	1.1	1.3	10.0	5.5	14.2	0.2	0.5	0.1	59.0	3.8
W6	20859	1999	CA	BE	1.3	0.7	0.9	11.0	5.9	14.8	0.1	0.8	0.1	57.0	4.1
W6	20860	1997	WA	BE	1.0	0.6	1.1	13.7	6.2	13.2	0.0	0.4	0.1	60.1	2.9
W6	20862	2004	CA	BE	1.3	0.8	1.2	14.4	5.4	15.3	0.0	1.5	0.1	53.2	5.6
W6	20865	1997	WA	BE	1.3	0.9	1.6	14.4	6.5	11.7	0.0	0.2	0.0	59.3	3.8
W6	20868	1995	WA	BE	0.7	0.3	0.6	13.6	6.3	13.7	0.1	0.6	0.0	58.6	4.4
W6	20869	2004	CA	BE	1.4	1.0	1.7	13.9	5.4	13.8	0.0	0.6	0.0	55.8	5.1
W6	20870	2004	CA	BE	1.3	0.6	1.5	13.7	5.6	13.1	0.2	0.2	0.1	58.2	4.0
W6	20871	2004	CA	BN	1.4	1.2	1.8	16.4	5.6	12.9	0.2	0.2	0.1	54.2	3.5
W6	20872	1995	WA	BN	1.3	0.9	1.3	15.0	6.9	12.1	0.1	0.6	0.0	56.8	2.5
W6	20873	1996	WA	BE	1.2	0.8	0.9	11.3	8.2	12.1	0.4	0.5	0.0	59.6	1.5
PI	279649	1997	WA	BE	1.3	0.8	1.6	15.0	3.4	11.7	0.0	1.1	1.3	57.6	4.4
PI	279650	2004	CA	BE	1.3	0.9	1.4	11.8	4.2	15.3	0.0	0.0	0.0	58.8	4.1
PI	283700	2000	CA	BN	1.2	0.8	1.5	13.2	4.2	12.2	0.0	0.3	0.0	60.5	3.8
PI	293005	2003	CA	BN	1.4	0.9	1.9	12.9	3.6	11.6	0.0	1.3	3.1	57.0	4.2
PI	293008	2000	CA	BN	1.3	0.9	1.6	13.8	4.7	11.3	0.0	0.0	0.0	60.2	3.0
PI	293010	1999	CA	BN	1.3	0.8	1.2	10.7	6.1	13.4	0.0	0.2	0.0	57.0	3.1
PI	293013	2000	CA	BE	1.1	0.8	1.4	13.8	6.2	12.1	0.0	0.3	0.0	61.2	2.8
PI	293015	2000	CA	BE	1.3	0.9	1.6	15.2	5.5	12.1	0.0	0.1	0.0	58.9	3.2
PI	293016	2003	CA	BE	1.3	0.5	1.2	15.2	5.2	13.3	0.0	0.3	0.0	58.7	3.2
PI	293027	1999	CA	BE	1.4	1.1	1.4	13.7	6.0	11.0	0.0	0.1	0.0	62.1	2.7
PI	293028	1999	CA	BE	1.3	1.0	1.4	12.4	5.9	12.3	0.0	0.3	0.0	60.8	3.5
PI	299412	1999	CA	BN	1.3	0.9	2.0	16.3	3.9	11.0	0.0	0.6	0.1	57.0	6.2
PI	331165	2002	CA	BN	1.4	1.0	1.6	14.6	6.3	13.2	0.0	0.6	0.0	57.2	3.6
PI	337050	2002	CA	BE	1.2	0.9	1.3	13.5	4.9	13.4	0.0	0.6	0.0	57.9	5.7
PI	355037	2003	CA	BN	1.6	1.0	1.5	17.9	5.0	5.8	0.0	1.0	0.8	62.9	1.8
PI	596362	2003	CA	BE	0.9	0.7	1.1	14.5	6.5	14.2	0.1	0.5	0.0	57.9	2.2
PI	596363	2003	CA	BE	0.9	0.5	1.1	14.2	6.4	13.9	0.0	0.3	0.0	59.3	2.2
PI	596364	2003	CA	BE	0.9	0.5	1.1	13.7	6.1	14.0	0.0	0.2	0.0	59.9	2.4
PI	596415	1995	WA	BE	0.7	0.6	0.9	10.5	5.8	8.7	0.1	0.5	0.0	43.2	1.6
PI	596416	1995	WA	BE	1.0	0.5	0.7	13.8	7.1	9.0	0.0	0.5	0.0	59.6	1.8
PI	596417	1996	WA	BE	1.0	0.5	1.1	14.0	6.9	9.0	0.0	0.5	0.0	58.4	2.2

PI	596418	1996	WA	BE	0.9	0.5	1.0	11.1	7.0	14.3	0.0	0.4	0.0	57.7	2.2
PI	596419	1996	WA	BE	1.0	0.4	1.1	16.4	7.7	14.1	0.0	0.5	0.0	55.5	2.1
PI	596420	2003	CA	BE	1.0	0.5	1.0	14.0	7.2	12.8	0.0	0.4	0.0	60.3	1.8
PI	596421	1996	WA	BE	1.4	0.6	1.9	15.0	6.2	12.3	0.1	0.2	0.1	58.6	2.1
PI	596422	1996	WA	BE	1.4	0.8	1.7	16.1	5.3	10.6	0.2	1.0	0.1	55.6	4.5
PI	596423	1996	WA	BN	1.7	0.5	1.1	15.1	7.6	14.1	0.1	1.2	0.2	52.7	4.2
PI	596424	1997	WA	BE	1.5	0.8	1.9	14.1	6.7	12.1	0.4	0.4	0.0	54.7	3.5
PI	596425	2003	CA	BE	1.5	0.9	2.0	13.2	6.5	11.7	0.3	0.7	0.1	55.4	3.6
PI	596426	1996	WA	BE	1.4	0.7	1.4	13.6	6.7	11.5	0.2	0.7	0.1	57.2	4.1
PI	596427	1996	WA	BN	1.4	0.6	1.4	14.6	7.3	12.3	0.3	1.3	0.2	54.1	3.7
PI	596428	1996	WA	BE	1.4	0.5	1.3	14.8	7.5	13.3	0.0	0.9	0.0	55.0	3.6
PI	596429	1996	WA	BE	1.3	0.6	1.7	12.8	7.2	11.4	0.3	1.0	0.0	57.4	2.9
PI	596430	1996	WA	BE	1.4	0.9	1.9	14.5	6.4	11.3	0.4	0.9	0.0	54.5	3.7
PI	596431	1996	WA	BN	1.6	0.7	1.4	15.4	7.7	12.5	0.1	1.1	0.1	54.1	3.5
PI	596432	1996	WA	BE	1.6	0.6	1.2	15.8	7.5	12.3	0.2	1.3	0.3	52.9	3.9
PI	596433	1997	WA	BE	1.4	0.8	1.5	14.4	5.1	12.3	0.3	0.8	0.1	55.4	4.2
PI	596434	1996	WA	BN	1.3	0.7	1.7	11.7	6.1	11.9	0.2	0.9	0.1	58.7	4.2
PI	596435	1996	WA	BE	1.7	1.6	1.8	15.5	6.4	11.0	0.4	0.6	0.0	54.1	2.8
PI	596436	1996	WA	BE	1.2	0.8	1.6	13.8	5.8	11.6	0.4	0.7	0.0	57.1	3.9
PI	596437	1995	WA	BN	1.8	2.2	2.0	12.7	6.3	11.2	0.6	0.9	0.1	54.0	3.5
PI	596438	1996	WA	BE	1.4	0.8	1.5	14.1	5.8	12.7	0.3	0.9	0.0	54.5	4.6
PI	596439	1996	WA	BE	1.1	0.7	1.5	13.3	5.6	11.6	0.3	0.6	0.0	57.7	4.2
PI	596440	1996	WA	BE	1.3	0.9	1.6	14.8	5.5	11.6	0.3	0.8	0.0	56.8	4.1
PI	596441	1996	WA	BN	1.6	1.3	1.7	11.8	7.1	12.0	0.4	0.6	0.0	57.0	3.5
PI	596442	1996	WA	BE	1.1	0.8	1.4	13.4	5.6	10.8	0.3	1.3	0.1	58.5	4.2
PI	596443	1996	WA	BN	1.2	0.9	1.4	12.9	5.6	11.1	0.4	0.7	0.0	59.1	4.0
PI	596444	1996	WA	BE	1.0	0.7	1.4	12.5	5.3	11.2	0.3	0.6	0.0	60.5	4.1
PI	596445	2003	CA	BE	1.2	0.8	1.3	13.5	4.9	11.8	0.1	0.8	0.0	58.7	5.1
PI	596446	1996	WA	BE	1.1	0.6	1.3	13.0	5.6	11.2	0.3	0.8	0.0	59.4	4.2
PI	596447	1996	WA	BE	1.1	0.7	1.5	13.1	5.5	11.3	0.4	0.6	0.0	58.5	4.0
PI	596448	1996	WA	BE	1.1	0.7	1.4	12.9	5.4	11.3	0.3	0.7	0.0	59.1	4.2
PI	596450	1996	WA	BE	1.4	0.7	1.2	14.1	6.5	10.6	0.1	1.0	0.1	58.9	3.7
PI	596452	1996	WA	BE	1.1	0.5	1.2	12.6	5.8	11.7	0.3	0.3	0.0	60.7	4.0
PI	596453	1996	WA	BE	1.3	0.8	1.7	12.7	6.1	11.0	0.6	0.4	0.0	57.2	3.9
PI	596454	1996	WA	BE	1.3	0.7	1.3	12.7	6.1	12.0	0.2	0.5	0.0	57.8	4.5
PI	596455	1996	WA	BE	1.4	0.8	1.4	13.1	6.0	11.7	0.4	0.0	0.0	57.8	3.7
PI	596456	1996	WA	BE	1.2	0.6	1.3	13.0	7.2	11.7	0.4	0.6	0.0	58.0	3.3
PI	596457	1996	WA	BE	1.0	0.5	1.0	12.6	6.7	12.1	0.3	0.5	0.0	60.4	2.6
PI	596458	1996	WA	BE	1.2	0.7	1.5	13.8	6.2	11.8	0.4	0.5	0.0	57.4	3.6
PI	596459	1996	WA	BE	1.3	0.7	1.5	14.3	5.6	10.2	0.3	0.6	0.0	59.5	3.7
PI	596460	1996	WA	BE	1.1	0.7	1.4	13.7	5.8	11.0	0.2	0.5	0.0	59.9	3.6
PI	596461	1996	WA	BE	1.4	0.9	1.4	14.7	4.9	11.6	0.2	0.5	0.0	57.0	3.7
PI	596462	1996	WA	BE	1.2	0.6	1.3	14.1	6.1	12.0	0.1	0.6	0.0	58.6	3.0
PI	596463	1996	WA	BE	1.1	0.7	1.5	13.3	5.7	11.3	0.3	0.8	0.1	58.5	4.1
PI	596464	1996	WA	BE	1.3	0.7	1.3	14.0	6.5	11.3	0.0	0.8	0.0	58.7	3.8
PI	596465	2003	CA	BE	1.4	0.7	1.3	14.3	6.0	11.8	0.0	0.9	0.0	58.1	4.2
PI	596466	1996	CA	BE	1.2	0.4	1.3	13.5	6.1	11.9	0.1	0.6	0.1	59.7	3.7
PI	596467	1996	WA	BE	1.4	0.8	1.4	15.5	5.9	10.4	0.1	0.9	0.1	57.5	4.0
PI	596468	1996	WA	BE	1.2	0.6	1.3	13.3	6.1	11.6	0.2	0.6	0.0	59.4	3.8

Table 2 – (Continued)

ID	Number	Harvest year	Location	Seed color	Fatty acid										
					Palmitic	Palmitoleic	Stearic	Oleic	Linolenic	Linoleic	Arachidic	Ricinoleic	Densipolic	Lesquerolic	Auricolic
PI	610492	2002	CA	BE	1.2	0.6	1.2	11.6	7.0	11.9	0.1	0.4	0.0	61.1	3.5
PI	613132	2003	CA	BE	1.3	0.9	1.4	14.8	5.7	12.9	0.3	0.3	0.0	55.7	4.8
PI	641918	2003	CA	BE	1.9	0.5	1.2	14.4	6.5	14.4	0.0	0.0	0.0	57.5	2.2
PI	641919	2004	CA	BE	0.9	0.5	1.2	15.2	6.0	13.9	0.0	0.3	0.0	57.8	2.3
PI	641920	2003	CA	BE	1.2	1.1	1.8	12.2	5.9	11.8	0.0	0.6	0.0	60.8	3.0
PI	641922	2003	CA	BE	1.4	0.6	2.0	12.9	6.7	13.0	0.0	0.3	0.0	58.5	2.8
PI	641923	2003	CA	BE	1.3	0.7	2.0	12.7	6.0	13.1	0.0	0.1	0.0	59.6	3.0
PI	641924	2003	CA	BE	1.4	0.8	1.9	12.9	6.1	13.4	0.0	0.3	0.0	58.4	3.3
PI	643170	2003	CA	BE	0.9	0.7	1.1	14.1	6.8	14.2	0.1	0.3	0.0	57.4	2.3
PI	643171	2003	CA	BE	1.0	0.3	1.2	18.5	5.7	12.9	0.0	0.2	0.1	55.5	2.0
PI	643176	2003	CA	BE	1.3	1.0	1.8	12.9	6.5	12.6	0.1	0.3	0.0	59.9	2.6
PI	643177	2003	CA	BE	1.5	0.5	1.7	12.2	6.0	12.8	0.0	0.7	0.0	59.6	3.1
PI	643179	2003	CA	BE	1.5	0.8	2.1	15.0	7.3	12.9	0.0	0.1	0.0	57.2	2.1
Mean ± S.E.					1.3 ± 0.1	0.8 ± 0.0	1.4 ± 0.1	13.8 ± 0.2	6.1 ± 0.1	12.0 ± 0.3	0.2 ± 0.2	0.6 ± 0.2	0.1 ± 0.7	57.9 ± 1.1	3.5 ± 0.4

S.E. – standard error; CA – California; WA – Washington, BE – beige; BN – brown.

sipolic, palmitic and palmitoleic acids was correlated to seed color. In *L. argyraea* seeds, only auricolic and ricinoleic acid content were influenced by both location and harvest year; harvest year was also significantly correlated to the content of linoleic and linolenic acids in accessions of the species.

In *L. argyraea*, only the content of auricolic and ricinoleic acids was significantly different for the two locations, whereas harvest year had an influence on the content of auricolic, linoleic, linolenic and ricinoleic acids. In this species, seed color had no influence on the content of the 11 fatty acids analyzed. In *L. gordonii*, seed color was a significant factor only for oleic, linoleic, linolenic and palmitoleic acids.

4. Discussion

Generally, the content of the fatty acids found in this study was slightly higher than the content reported in the literature (Dierig et al., 1996; Salywon et al., 2005). This may be a result of environmental effects of these locations on the fatty-acid contents. Although, Dierig et al. (2006a,b) reported no significant differences in fatty-acid contents of *L. fendleri* seeds grown at three sites ranging in elevation from 300 to 1219 m, some differences were observed for *L. pallida* (affin.) when grown at the lower (300 m) elevation. In our study, a significantly higher yield of selected fatty acids was observed in *L. fendleri* seeds harvested in the warmer California location. In soybean [*Glycine max* (L.) Merr.], the fatty-acid composition in seeds was affected by environment, years and planting dates (Cherry et al., 1985; Schnebly and Fehr, 1993; Ray et al., 2008). Future agronomic studies with *Lesquerella* may show a similar effect. Different analytical techniques, different maturity of seeds used for the analyses (Miquel and Browse, 1995; Salywon et al., 2005) and the genetic diversity of the accessions may also have played a role in the study differences.

The highest content of lesquerolic acid reported by Salywon et al. (2005) for unimproved *Lesquerella* germplasm was in *L. pallida* 79.8% (accession no. 3219i). In our study, lesquerolic acid content in *L. pallida* was 84.6% (W6 20847). In *L. fendleri*, the range reported by Salywon et al. (2005) was 25.1–58.2% (mean 51.4%); in our study, the range for the 104 *L. fendleri* accessions was 43.3–66.3% (mean 57.9%). In some S_1 breeding lines of *L. fendleri* the lesquerolic acid content was up to 76.5% (Dierig et al., 2006a,b), i.e., much higher than in unimproved germplasm. Hayes et al. (1995) reported 41–47% of densipolic acid in *Lesquerella* seeds, while Salywon et al. (2005), reported densipolic acid content in *L. densipila*, *L. lescurii*, *L. lyrata*, *L. perforata*, and *L. stonensis* of 33.7, 34.8, 26.9, 35.2, and 15.8%, respectively. In our study, for the same species the highest content of densipolic acid was 46.8, 43.3, 43.4, 47.1, and 45.0%, respectively, which is comparable to data presented by Hayes et al. (1995). Auricolic acid content in *L. auriculata* was also much higher in our study (average 39.5%) than reported by Salywon et al. (2005; 16.1%), but was similar to data reported by Kleiman et al. (1972) and Hayes et al. (1995). No densipolic or ricinoleic acid was found in *L. ludoviciana* by Salywon et al. (2005); in our study, a single accession of *L. ludoviciana* contained 14.0 and 6.2% of these respective acids, whereas Hayes et al. (1995) reported 10.0 and 13.0% for densipolic and ricinoleic acids for this species.

Table 3 – Effect of seed growing location, harvest year and seed coat color on fatty-acid content (%) in three species of *Lesquerella* germplasm

Fatty acid	*L. fendleri* (~7400 plants)			*L. argyraea* (~790 plants)			*L. gordonii* (~1200 plants)		
	Location	Harvest year	Seed color	Location	Harvest year	Seed color	Location	Harvest year	Seed color
Lesquerolic	**	*	ns	ns	ns	ns	ns	ns	ns
Densipolic	ns	ns	**	ns	ns	ns	ns	ns	ns
Auricolic	ns	*	ns	**	**	ns	ns	ns	ns
Oleic	ns	ns	ns	ns	ns	ns	ns	ns	*
Linoleic	**	*	ns	ns	**	ns	ns	ns	*
Linolenic	**	**	ns	ns	**	ns	ns	ns	*
Ricinolenic	**	**	ns	**	**	ns	ns	ns	ns
Stearic	ns	ns	ns	ns	ns	ns	ns	ns	ns
Palmitic	ns	ns	**	ns	ns	ns	ns	ns	ns
Palmitoleic	ns	ns	**	ns	ns	ns	ns	ns	*
Arachidic	**	**	ns	ns	ns	ns	ns	ns	ns

*<0.05; **<0.01; ns – not significant.

Statistically, the content of lesquerolic and auricolic acids in *L. fendleri* was similar across 101 and 97 accessions, respectively. For improvement of lesquerolic or auricolic fatty acids, it would not matter which of the 101 or 97 accessions are used; however, these accessions may be different for other characteristics not yet evaluated. The current NPGS genetic pool of *L. fendleri* supports an improvement of lesquerolic hydroxy fatty acid up to 66.3% and below 10% of unsaturated fatty acids (linolenic and linoleic). Other species may contribute to the improvement of lesquerolic HFA in *Lesquerella* cultivar development to over 80% (*L. lindheimeri* and *L. pallida*) and to low values of unsaturated fatty acids (ca. 2%, *L. stoniensis* and *L. grandiflora*).

Our study represents the first extensive report on the profile of the four hydroxy fatty acids and the seven other fatty acids occurring in seed of *Lesquerella* germplasm publicly available. It provides information to *Lesquerella* germplasm users along with evidence that levels of certain fatty acids were influenced by harvest year, growing location and seed color. The data may aid breeders in selection of species and accessions for the crop breeding programs. Apparently, other than *L. fendleri* species may provide genetic material for the crop improvement. The NPGS *Lesquerella* germplasm collection is diverse for the content of the 11 fatty acids analyzed, and it provides a good source of genetic variation for selection and research purposes. Twenty species (62.5%) in the collection, however, are represented by only one or two accessions, and collection of additional germplasm for those species may be needed to support the development of high fatty acid producing *Lesquerella* cultivars. Experimentation on the influence of the plant growing environment as well as establishing possible correlations between morphological characteristics of the seeds and the fatty-acid content may accelerate future development of *Lesquerella* as an economic crop for arid-land agriculture.

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